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TRIBAL AND SUBTRIBAL  
DELIMITATION AND  
CIRCUMSCRIPTION OF THE  
GENERA OF ARACEAE  
TRIBE LASIEAE<sup>1</sup>

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ABSTRACT

The Lasieae, comprising a relictual pantropical tribe of aroids, are defined and described. Four subtribes are recognized: neotropical Dracontiinae (*Dracontioides* Engl., *Dracontium* L., and *Anaphyllopsis* A. Hay), Indochinese Pycnospathinae (*Pycnospatha* Thorel ex Gagnepain), Indian Anaphyllinae A. Hay described herein (*Anaphyllum* Schott), and pantropical Lasiinae (*Cyrtosperma* Griff., *Lasia* Lour., *Lasiomorpha* Schott, *Podolasia* N. E. Br., and *Urospatha* Schott). Keys and diagnoses are given for the subtribes and genera, and the latter are described. Seeds are illustrated. Geography of the tribe is discussed; it is suggested that the group is Gondwanan in origin and that, in the Orient, it has arrived in Malesia from both the East and the West. *Dracontium polyphyllum* L. is lectotypified. The combination *Dracontium schomburgkii* (Schott.) A. Hay is made following the reduction of *Echidnium* Schott.

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The Lasieae are of critical interest in the Araceae as a relictual pantropical group that shows great range of leaf form, from highly compound to lanceolate, and spathe form from campanulate to hood-forming to bractlike. The flowers show the greatest range in numbers of parts in any hermaphrodite-flowered aroid group. The leaves are frequently armed, a condition to which Corner (1949 et seq.) has drawn attention as a putatively primitive one, and they show an acropetal method of leaf expansion of restricted systematic distribution in Araceae, and of very rare occurrence in the monocotyledons as a whole (Hay, 1986). Two of the four subtribes have extremely restricted distributions, as have nearly half the genera and many of the species—factors that may indicate an ancient group in decline (Scott & Day, 1983).

The group appears to represent a primitive clade of Araceae. While the hermaphrodite tepalate flowers suggest also a primitive grade (in this respect), the Lasieae are nevertheless highly heterobathmic

and are thus a vitally important source of information contributing to the development of hypotheses of evolutionary trends in the family as a whole. Indeed, study of this group, particularly in the Old World, has led Hay (1986) and Hay & Mabberley (in press) to propose a radically new hypothesis for the origin of the Araceae.

A cladistic treatment has not been attempted, both for philosophical reasons and for the pragmatic one that one of the larger neotropical genera (*Urospatha*) requires a monograph before its characterization can be established. This work resolves a number of problems in the generic delimitation of the Lasieae and serves to highlight others.

HISTORICAL BACKGROUND

THE GENERA

Of the five species of *Dracontium* in Linnaeus's *Species Plantarum* (1753), two are recognized today as belonging in the tribe Lasieae—*D. poly-*

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*phyllum* and *D. spinosum*. The remaining three are *Monstera pertusa* (L.) de Vries, *Symplocarpus foetidus* (L.) Nuttall, and *Lysichiton camtschatcensis* (L.) Schott, the first in subfamily Monsteroideae, the latter two considered by Krause (1908) to belong in subfamily Calloideae. Rafinesque (1838) said of Linnaeus's *Dracontium* species that "the scandent species appear the type of *Dracontium* which Adanson changed to *Monstera* perhaps a better name," and so he superfluously renamed *D. polyphyllum* as *Eutereia nigricans* Raf.

In 1790 Loureiro based the genus *Lasia* on a plant collected from near Hanoi, Vietnam. The type species, *L. aculeata*, was recognized by Thwaites in 1863 to be conspecific with Linnaeus's *D. spinosum*, and the new combination *L. spinosa* (L.) Thwaites was made.

In 1851 Griffith described *Cyrtosperma* for a plant from the Malay Peninsula. Then came Schott, who erected *Urospatha* in 1853 for seven neotropical species (including a *Sagittaria*—"U. *friedrichsthali*"). These (except *U. friedrichsthali*) are now included in *U. sagittifolia* (Rudge) Schott, which Rudge had described as a species of *Pothos* in 1805 based on a plant collected in Guyana by Martin. In 1857 Schott based *Lasiomorpha* on an African plant and *Arisacontis* on a Pacific one collected by Chamisso (which had already appeared in 1837 without a diagnosis as *Apereoa* Moerenhout). Engler later combined both of these genera with *Cyrtosperma*. *Lasiomorpha* is resurrected here. Also in 1857, Schott based *Ophione* and *Echidnium* on neotropical plants subsequently included in *Dracontium* by Engler (1911) and Bogner (1985) respectively. In 1858 he described *Anaphyllum* based on an Indian plant. Later, in 1865, he extracted his rival K. Koch's *D. asperum*, described the genus *Chersydrium*, and applied the superfluous epithet "*jararaca*," a local name noted also by Spruce (1908) and referring to the snakelike petioles characteristic of the genus. In 1869, Seemann named the gigantic Nicaraguan and Costa Rican geophyte *Godwinia gigas*, which ten years later Engler reduced to sectional status in *Dracontium*. In 1882 N. E. Brown described *Podolasia* from material obtained from Borneo and cultivated in England by Veitch.

Engler (1911) extracted Schott's *Urospatha desciscens* in describing the monotypic east Brazilian genus *Dracontioides*. In 1941, Gagnepain published the genus *Pycnospatha*, described in manuscript by Thorel for two species of atepalate geophytes from Laos and Thailand. Hay (1988a) has erected the neotropical genus *Anaphyllopsis* based on a species of Engler's heterogeneous pan-

tropical *Cyrtosperma* and two new species. Bunting (1988) has created *Urospathella* for a diminutive Venezuelan savanna herb, which is reduced here to synonymy with *Urospatha*.

#### SUPRAGENERIC GROUPINGS

Schott (1832, 1858, 1860) was the first specialist to arrange the genera of Araceae, putting in a widely expanded tribe "Orontieae" the genera *Chersydrium*, *Dracontium*, *Echidnium*, *Ophione*, and *Urospatha* (together with *Symplocarpus*) in his subtribe Dracontiinae next to his subtribe Lasiinae, which included *Anaphyllum*, *Arisacontis*, *Lasia*, and *Lasiomorpha*.

Engler's reappraisals (1877, 1879, 1911) were based on considerably more material and phylogenetic concepts. He perceived that neither *Orontium* nor *Symplocarpus* had close relationship with the remaining genera, and he combined Schott's subtribes into his (Engler's) Lasieae, at the same time (1877) erecting the subfamily Lasioideae. Ultimately he abandoned subtribal classification. Hutchinson (1934) elevated Schott's subtribes Lasiinae and Dracontiinae to tribal rank, for some unspecified reason including the monsteroid genus *Holochlamys* in his concept of Dracontieae. Subsequently Nakai (1943) recognized Lasieae (ovary unilocular) as including *Anaphyllum*, *Lasia*, and *Podolasia*; erected "Urospatheae" (ovary 2-6-locular; the name Dracontieae was already available) to include *Dracontioides*, *Dracontium*, and *Urospatha*; and erected Cyrtospermateae for *Cyrtosperma*, the latter based solely on the character of dehiscent fruit, which he presumably obtained from Engler's inaccurate illustration (1911, fig. 7f) of dehiscent fruits in *C. lasioides* Griff. Neither Hutchinson's nor Nakai's classification of Araceae has had much following by specialists.

When he published *Pycnospatha*, Gagnepain, on the basis of its atepalate flowers, allied it with the north temperate bog-dwelling *Calla*, an affinity which Bogner (1973) denied, noting the greater resemblance to *Dracontium*. Bogner included *Pycnospatha* in Lasieae (sensu Engler), regarding the atepalous condition as sufficient to warrant erecting the monogeneric subtribe Pycnospathinae, and in so doing re-created Lasiinae for the remaining genera. However, it is proposed here that the genera of Lasiinae (sensu Bogner) are sufficiently diverse to warrant either rejecting Bogner's recognition of subtribal status for *Pycnospatha* or subdividing Lasiinae (sensu Bogner) further to reflect the variation. The latter course is adopted here since this best portrays a close-knit and relictual tribe. The

subtribes proposed are based on vegetative architecture, leaf, seed, and flower morphology, and distribution.

Within his classification of the family, Engler (1877 et seq.) regarded the Pothoideae and Lasioideae as occupying central positions, separating them on anatomical grounds (laticifers present and absent respectively). He regarded *Pothos* as the most primitive genus in the family. The Lasioideae he regarded as more specialized, being generally more elaborate and sometimes with more specialized floral construction. He recognized hermaphrodite-flowered and monoecious groups in the subfamily, the former represented by the Lasieae, the latter by the Thomsonieae (*Amorphophallus*, *Anchomanes*, *Plesmonium*, *Pseudodracontium*, *Pseudohydrosme*, and *Thomsonia*), Nephthytideae (*Cercestis*, *Nephthytis*, and *Rhektophyllum*), and Montrichardieae (*Montrichardia*).

Grayum (1984, 1990), on palynological and other grounds, has suggested that *Amorphophallus*, *Pseudodracontium*, *Plesmonium*, and *Thomsonia* be moved from Lasioideae to Aroideae. He further suggested that *Anchomanes* and *Pseudohydrosme* are more closely allied with Nephthytideae, and that Montrichardieae and Nephthytideae may belong nearer Philodendroideae. He tentatively allied Lasieae with Stylochaetoneae (extracted from Engler's Aroideae) and *Symplocarpus* (thitherto considered a member of the enigmatic Calloideae). He concluded that subfamily Lasioideae may be recognized to include three tribes: boreal Orontieae (*Symplocarpus*, *Lysichiton*, *Orontium*), Lasieae (as here), and African Stylochaetoneae (*Stylochaeton*). Of these, further evidence is necessary to verify that Orontieae are natural, and there can be little doubt that if these groups form a monophyletic unit it is a profoundly fragmented one.

The great strength of Engler's system is its classification at tribal level, which largely stands today. Arguably it is better to begin formal division of the Araceae at the level of tribe rather than subfamily, and to talk of informal tribal alliances.

#### LASIEAE

**Lasieae** Engler, Nova Acta Acad. Leopold.-Carol. 39:144. 1877.

Massive to slender cormous, rhizomatous, or suffruticose terrestrial or semiaquatic plants; stems erect to creeping, sympodial, the modules bearing a prophyll, one to several euphylls and sometimes

one or more cataphylls<sup>3</sup>; internodes distinct and then sometimes armed, or very condensed. Leaves small (measured in centimeters) to enormous (a few meters in length), solitary or spirally clustered, with the petioles and blades often armed with scattered or flanged spines or variously spinescent warts, often conspicuously mottled and streaked; blades highly compound to pinnate, hastate, or lanceolate, frequently fenestrate, or with the lobes developed marginally, or both; maturation of the whole leaf markedly acropetal, the blade exposed from the bud at an early stage in its expansion (Fig. 1); venation reticulate; rachis and/or petiole sometimes geniculate; sheath short, infrequently up to ca. 20% of the length of the petiole. Inflorescence solitary, very rarely (and then irregularly) in a cymose pair; peduncles mostly similar in length and texture to the petioles, occasionally much abbreviated; spathe campanulate to hood-forming to spirally twisted to  $\pm$  bractlike, occasionally armed outside or papillate within, mostly purple-brown, often streaked yellowish, rarely pink or white, persistent, marcescent or caducous; spadix usually shorter than the spathe, stipitate or sessile, mostly a direct continuation of the peduncle, sometimes with the stipe adnate to the adaxial side of the spathe; maturation of flowers and fruits in a basipetal sequence (Fig. 2). Flowers hermaphrodite throughout the spadix, rarely the apical ones sterile (*Dracontium*), (9-)6-4-tepalate (0 in *Pycnospatha*); tepals free, imbricate; stamens 4-12 with distinct anthers and free filaments (except *Lasiomorpha*); anthers extrorse, dehiscent by longitudinal slits to  $\pm$  apical pores; pollen extruded in ropelike masses, ellipsoid, monosulcate with usually reticulate exine, binucleate and starch-free; ovary 1-6-locular, superior to slightly inferior (*Lasiomorpha*), the locules uni- to multiovulate; placentation axile, basal, parietal or apical; ovules bitegmic, anatropous; stigma buttonlike, unlobed, microscopically papillate or verruculate, wet with or without a pollination droplet, style distinct or none. Fruit with rudimentary spines (*Lasia*, *Pycnospatha*) or smooth, indehiscent, usually a red berry, 1-several-seeded, ovoid to obpyramidal, sessile on the spadix, rarely expelled (as in *Anthurium*). Seed pachychalazal (sensu Corner, 1976), often with "tegmic" and "testal" layers differentiated within the pachychalaza, hard,  $\pm$  campylotropous, reni-

<sup>3</sup> A prophyll is distinguished from a cataphyll by its position at the beginning of an axis and by its bicarinate structure.



FIGURE 1. a. An emerging leaf in *Dracontium polyphyllum*. — b. The blade undergoes some tenfold increase in length during expansion after it has emerged from the cataphylls. Cultivated at the Bogor Botanic Gardens.

form to helical, with an oily strophiole or rudimentary aril at the chalazal end; ovular integuments with the true micropyle forming an operculum over the pachychalazal micropyle; seed coat variously spiny, crested, warty, or smooth; (in *Anaphyllum*, seed ovoid, seed coat membranous); endosperm present or absent;  $n = 13$ , or 26 (*Urospatha*).

*Differential characters.* Terrestrial or semi-aquatic habit, early leaf exposure, reticulate venation, basipetal flower and fruit maturation, hermaphrodite flowers, campylotropous pachychalazal seeds, monosulcate heteropolar binucleate, starch-free pollen monads (Grayum 1984: 275–280),  $x = 13$  (Marchant, 1973; Petersen, 1989).

*Distribution.* Pantropical with subtropical extensions into the Himalayan foothills (*Lasia*); absent from Australia. Distribution is discussed below.

*Ecology.* Lowland, rarely montane; on floor and edge of and gaps in rainforest, monsoon forest, and semideciduous forest, to open, mostly swampy, sites. Cormous species are sometimes tolerant of

seasonal drought. Inflorescences generally present a saproentomophilous pollination syndrome of dark coloration and the smell of decaying organic matter.

Ray (1987) has published a classification of aroid shoot diversity. In his terminology, the axes in Lasieae are anisophyllous sympodial. Growth of the renewal axis after flowering is sylleptic in the subtribe Lasiinae, and hence each module bears first a prophyll, and the subsequent leaf (the mesophyll) and all other leaves are foliage leaves. In the genera of the remaining subtribes, growth of the renewal axis after flowering is proleptic (with the possible exception of *Dracontioides*), and hence at least the mesophyll has the form of a cataphyll. Where flowering occurs after a period of dormancy, the inflorescence is subtended by a number of bracteoles (*Dracontium*, *Pycnospatha*). Inflorescences are generally solitary throughout the tribe. Where they are paired (in vigorous individuals of certain species, e.g., *Anaphylloopsis americana* (Engler) A. Hay, *Cyrtosperma macrotum* Becc. ex Engler) they are multiplied according to an axillary mo-



FIGURE 2. Basipetal fruit maturation in the spadix of *Anaphyllum wightii* (Hay s.n., FHO). Anthesis also takes place in a basipetal sequence in Lasieae.

nophyllous sympodial plan in *Cyrtosperma*, and have an interposed mesobracteole and bracteole in *Anaphyllopsis* between the subtending prophyll of the second inflorescence and the base of its pe-

duncle. In Ray's system an essentialist's stance is adopted, and the term "leaf" is used for several functionally quite different organs. In the present work, "leaf" means foliage leaf.

KEY TO THE SUBTRIBES

- 1a. Flowers atepalate, plant cormous, leaf solitary, spathe hood-forming, fruit spinous, seed coat with raphides and druses ..... Pycnospathinae
- 1b. Flowers tepalate, other characters not in the above combination.
  - 2a. Stems bearing prophylls and euphylls only ..... Lasiinae
  - 2b. Stems bearing cataphylls and prophylls.
    - 3a. Seed ovoid, smooth, coat membranous; stems clump-forming to rather weakly stoloniferous, leaves never fenestrate ..... Anaphyllinae
    - 3b. Seed  $\pm$  campylotropous; coat hard, ornate; leaves often fenestrate ..... Dracontiinae

SUBTRIBE 1. DRACONTIINAE SCHOTT

**Dracontiinae** Schott in Schott & Endl., Melet. Bot. 22. 1832. "Dracontiae."

Cormous or rhizomatous, usually solitary herbs. Stems cataphylliferous (?except *Dracontioides*). Leaves usually solitary or paired (except *Dracontioides*), with usually warty, or rarely spiny petioles; blades often highly compound and/or fenestrate, rarely simple and entire. Spathe erect, hood-forming or spirally twisted. Flowers tepalate. Seed campylotropous, albuminous; seed coat thick, usually ornate.

*Distribution.* Three genera ranging from southern Mexico, through Central America to Brazil, southeast to near Rio de Janeiro.

KEY TO GENERA

- 1a. Leaves clustered, sagittate, fenestrate with the holes not reaching the margin; spathe hood-forming, ovary bilocular ..... *Dracontioides*
- 1b. Leaves solitary or two together, ternately divided to highly compound.
  - 2a. Plants cormous; leaves highly compound or if not, then with the posterior lobes each equally bifid; spathe usually erect to hood-forming, sometimes campanulate ..... *Dracontium*
  - 2b. Plants rhizomatous; leaves sagittate and divided by fenestration to pinnate by marginal dissection; spathe spirally twisted ..... *Anaphyllopsis*

**Dracontium** L., Sp. Pl. 967. 1753. TYPE: *D. polyphyllum* L. [Type: Hermann, *Paradisus Batavus*, fig. 93. 1698 (lectotype, selected here).]

*Eutereia* Raf., Fl. Tellur. 4: 12. 1838, nom. superf. pro *Dracontium*. TYPE: *E. nigricans* Raf., nom. superf. pro *D. polyphyllum*.

*Echidnium* Schott, Oesterr. Bot. Wochenbl. 7: 62. 1857.

- TYPE: *E. schomburgkii* Schott = *Dracontium schomburgkii* (Schott) A. Hay, comb. nov.
- Ophione* Schott, Oesterr. Bot. Wochenbl. 7: 101. 1857. TYPE: *O. purdieana* Schott = *D. purdieanum* (Schott) Engl.
- Chersydrium* Schott, Oesterr. Bot. Zeitschr. 15: 72. 1865. TYPE: *C. jararaca* Schott, nom. superf. pro *D. asperum* K. Koch.
- Godwinia* Seemann, J. Bot. 7: 313, t. 87, 96. 1869. TYPE: *G. gigas* Seemann = *D. gigas* (Seemann) Engl.

Gigantic to slender cormous herbs, with solitary, rarely paired, compound to highly compound leaves; corm hemispherical or  $\pm$  irregular, concave around the bud, roots arising mostly from the top, commonly bearing scattered to very numerous small bulbils. Leaf to 5 m tall, subtended by several evanescent cataphylls, emerging from these in a very unexpanded state and thereafter undergoing a long exposed period of great expansion; petioles mottled, usually warty, the warts rounded,  $\pm$  pointed to spinous; blade tripartite, to 4 m across, the petiole divided into three subequal rachises; of these, the anterior undergoing at least one more 3-parted division and forming a pair of opposite lateral secondary rachises, and a continuation of the anterior rachis; posterior rachises forked, rarely not further divided; ultimate branches of the rachises bearing  $\pm$  pinnately arranged sessile, ovate to rhomboid, or rarely linear leaflets; in addition the rachises bearing scattered leaflets throughout; leaflets with pinnate, brochidodromous venation, often fenestrate, rarely the whole blade entire in bud, the parts separating on expansion, and then the leaflets truncate. Inflorescence solitary, accompanying or alternating with the leaf; peduncle exceeding, equaling or shorter than the petiole, sometimes not extending above ground level, when long similar to the petiole; spathe mostly purple-brown, campanulate to hood-forming to erect, occasionally somewhat twisted in uppermost part, smooth or papillate within; spadix sessile to stipitate, usually disproportionately small, sometimes with the uppermost flowers with enlarged tepals, forming a short appendix bearing ascidiform structures (Fig. 4), putrid-smelling over a lengthy period. Flowers 9-6-tepalate, 12-6-staminate; ovary 6-1-locular, often bearing a long style (to ca. 6 mm); locules 1-few-ovulate; stigmas papillate or not, wet. Fruit mostly obpyramidal, red, smooth, usually accompanied by the  $\pm$  marcescent spathe, often beaked with the persistent style. Seed campylotropous, crested and/or warty, inner layers of pachychalaza with cell walls thicker than those of the outer ones; endosperm present (Figs. 5a, 6a).



FIGURE 3. Lectotype of *Dracontium polyphyllum* L., from P. Hermann, *Paradisus Batavus* (1698) figure 93.

*Typification of Dracontium polyphyllum.* Of the elements cited in Linnaeus's *Species Plantarum*, material of this plant in the Clifford Herbarium is sterile and fragmentary. The figure in Plukenet's *Almagestum* (1696, t. 149, fig. 1) is highly stylized, while that in Hermann's *Paradisus Batavus* (1698, fig. 93), reproduced here (Fig. 3), is clearly *D. polyphyllum* in the current sense—with a short peduncle, hood-forming spathe, prominent styles, and no (or few) fenestrations in the leaflets. This illustration is therefore here selected as lectotype.

*Distribution.* About 15 species from Chiapas, Mexico, through Central America and tropical South America, predominantly in open sites, also in rain-forest, tolerant of seasonal drought; mostly at low altitude.

This genus is in need of revision. It shares with Old World *Amorphophallus* the problem of matching fertile and sterile material in those species in which flowering and leafing alternate. This will entail extensive fieldwork and use of living collections. Several species are in cultivation at St. Louis, Kew,

and Munich. Most species appear to have very restricted distributions, although this may in part be due to insufficient collecting. Madison (1978) noted that *Dracontium* species tend to occur as rare, easily overlooked single individuals, although the bulbiferous species form substantial clumps.

There is no available information on the pollination biology. Inflorescence color, smell, and morphology suggest saprocanthrophily and sapromyophily. The Panamanian *Dracontium dressleri* Croat, in cultivation at Kew emits an odor of stale meat and dirty socks over a period of about three weeks, in marked contrast to the brief exhalations of the quickly acting monoecious groups (e.g., Meeuse, 1978) and recalling the behavior of *Symplocarpus* (Knutson, 1974). Peduncle lengths ranging from none in *D. dressleri*, for example, to ca. 1.5 m in the Colombian *D. carderi* Hook. f. suggest selection for different pollinators. So do the markedly differing style lengths, where stigmas may be more or less sessile, for example in the recently described Venezuelan *D. changuango* Bunting (Fig. 1), or borne on long styles as in *D. polyphyllum* and *D. gigas* (Engler, 1911). (Long styles are unusual in the Araceae.)

The morphology of the spadix apices in some species is curious. The Mexican *D. soconuscum* Matuda and *D. changuango* have one to several (or sometimes no) stalked asciform structures in place of the upper flowers (Fig. 4), whereas in *D. dressleri* tepals of the upper flowers are much longer than those of the rest, as is sometimes the case in *Cyrtosperma cuspidispathum* Alderw.

*Dracontium* fruits are characteristically obpyramidal, the upper part of the fruit showing upward and outward expansion above the locules. Similar fruits occur in *Anaphyllopsis americana* (Engler) A. Hay and, less expanded, in *Dracontioides* and *Lasia*. In other Lasieae and in most aroids the pericarp is more even in thickness throughout.

The leaves defy succinct description. Those of the Nicaraguan and Costa Rican *D. gigas* rank with the largest of all, outside the palms, reaching some five meters in height and four meters in blade diameter. In contrast, *D. margaretae* Bogner from Brazil, Venezuela, Bolivia, and Paraguay is a comparatively dwarf species in which the posterior and anterior lobes are only once divided into linear leaflets (Bogner, 1981). Engler (1911) noted that the leaves of *D. gigas* and *D. costaricense* Engl. are entire in bud, and the whole is segmented from within the lamina, as in the similarly elaborate leaves of *Anchomanes* and *Pseudohydrosme*. In *D. polyphyllum*, the main lobing of the leaf ap-

pears marginal, and the ultimate divisions are intramarginal, occasionally failing and leaving fenestrate leaflets. These observations are based on unfolding and mature blades, and further evidence of early developmental stages is required.

A striking feature of *Dracontium* leaves is their early emergence from the cataphylls. The branches and segments of the anterior lobe are bunched and point upward in bud, together with the inner/upper product of the first division of each posterior lobe; the outer/lower half is similarly bunched, but points down the petiole. Expansion proceeds over a period of weeks in an acropetal wave up the petiole to the blade; this is in marked contrast to the otherwise rather similar leaves of *Amorphophallus*, which emerge in a late stage of apparently diffuse rather than polar expansion. Mottling is streaked in *Dracontium* versus usually maculate in *Amorphophallus*, perhaps reflecting their differing methods of expansion.

**Dracontioides** Engl., Pflanzenr. IV. 23C: 36. (Heft 48). 1911. TYPE: *D. desciscens* (Schott) Engl. [Basionym: *Urospatha desciscens* Schott, Oesterr. Bot. Zeitschr. 9: 99. 1859. Type: Brazil. Bahia: Salvador, Itaparica, Riedl 714 (holotype, LE not seen; isotype, K).]

Robust to rather slender swamp herbs to ca. 2 m high; rhizome erect, sparsely branching, to 40 cm long and ca. 6 cm diam., bearing a crown of several sagittate rarely  $\pm$  ovate and then auriculate leaves. Leaf blades glossy, in larger leaves fenestrate; fenestrations more numerous in anterior than in posterior lobes; petioles smooth to rough, mottled brownish and green, unarmed, watery, drying thin, with large numbers of easily detached bulbils in their axils; cataphylls present, but very short (shorter than sheath of petiole); sheath membranous. Inflorescence solitary on a peduncle similar to but usually shorter than the petioles; spathe forming a deep hood, brownish green without, deep purple and longitudinally streaked yellowish, becoming pink toward the base, within to 15 cm long; spadix much shorter than the spathe, sessile to shortly stipitate, purple. Flowers 4-tepalate; stamens 4, exerted from the tepals at male anthesis; ovary bilocular with a purple conical style; locules uniovulate with axile placentation; stigma buttonlike, whitish, wet. Fruit reddish, furrowed, usually 2-seeded. Seeds campylotropous, asymmetrical with the micropylar end longer and narrower than the chalazal end, albuminous; seed coat thick, hard, brown with up to 8 sharp longitudinal warty crests (Figs. 5b, 6b).

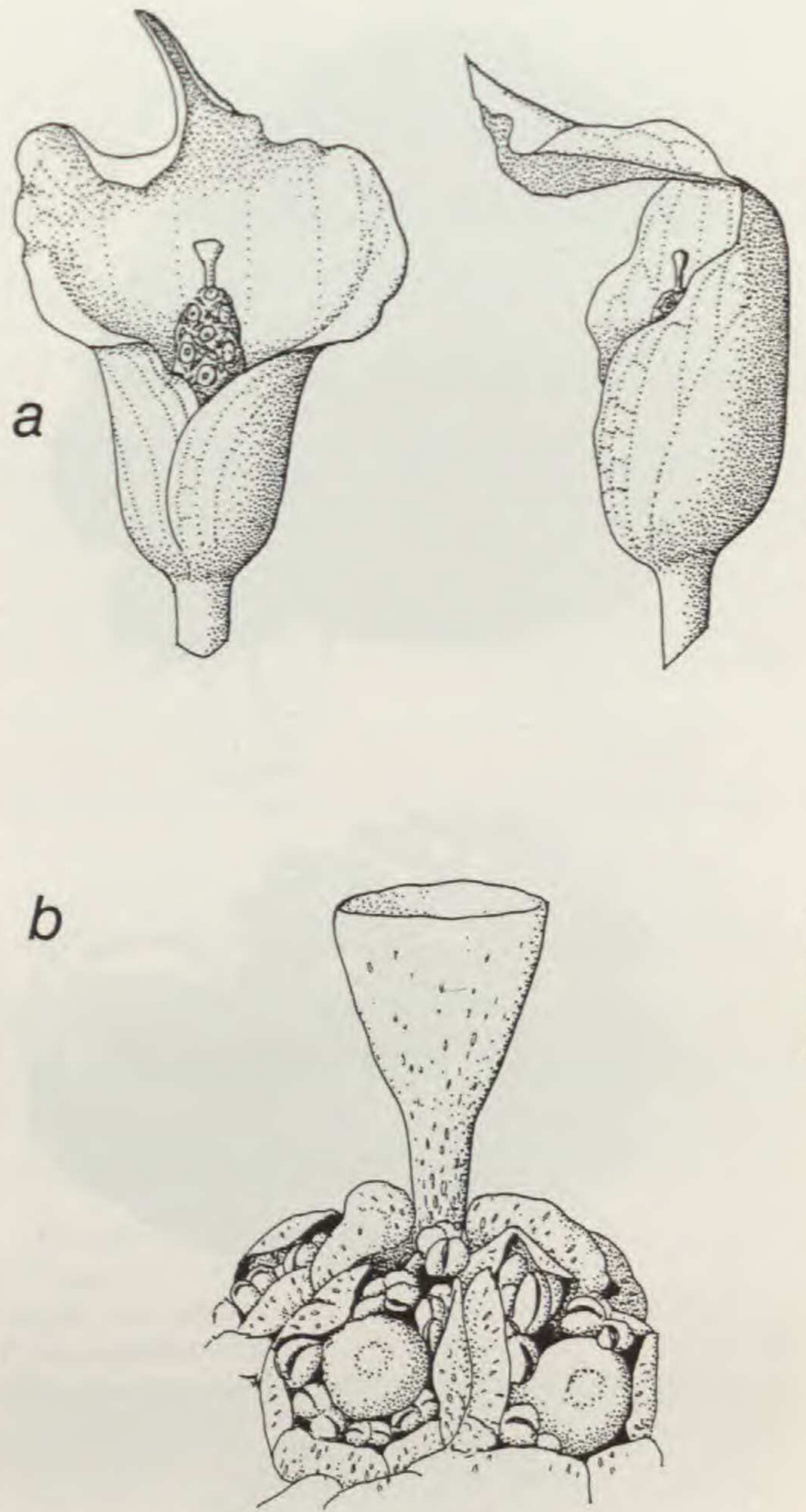


FIGURE 4. The spadix apex of *Dracontium changuango* (Aristeguieta 12734, K).—a. The whole inflorescence; scale bar = 2 cm.—b. Apical flowers; scale bar = 3 mm.

**Distribution.** Riverbanks, swamps, and swamp forest undergrowth in rainforests of eastern Brazil, in Bahia, and near Rio de Janeiro at Tijuca (Mayo, 1978).

Schott (1859) ascribed this species to *Urospatha* because of the bilocular ovary that characterized all species of *Urospatha* then known in the fertile state. Engler, however, noted the albuminous seed (*Urospatha* species were exalbuminous), and that the hood-forming spathe more closely resembled that in *Dracontium*, hence the name *Dracontioides*. The spathe, the fenestrate leaves, and the presence of bulbils indicate closer affinity with *Dracontium* than with any member of the Lasieae, and the seed and vegetative architecture warrant



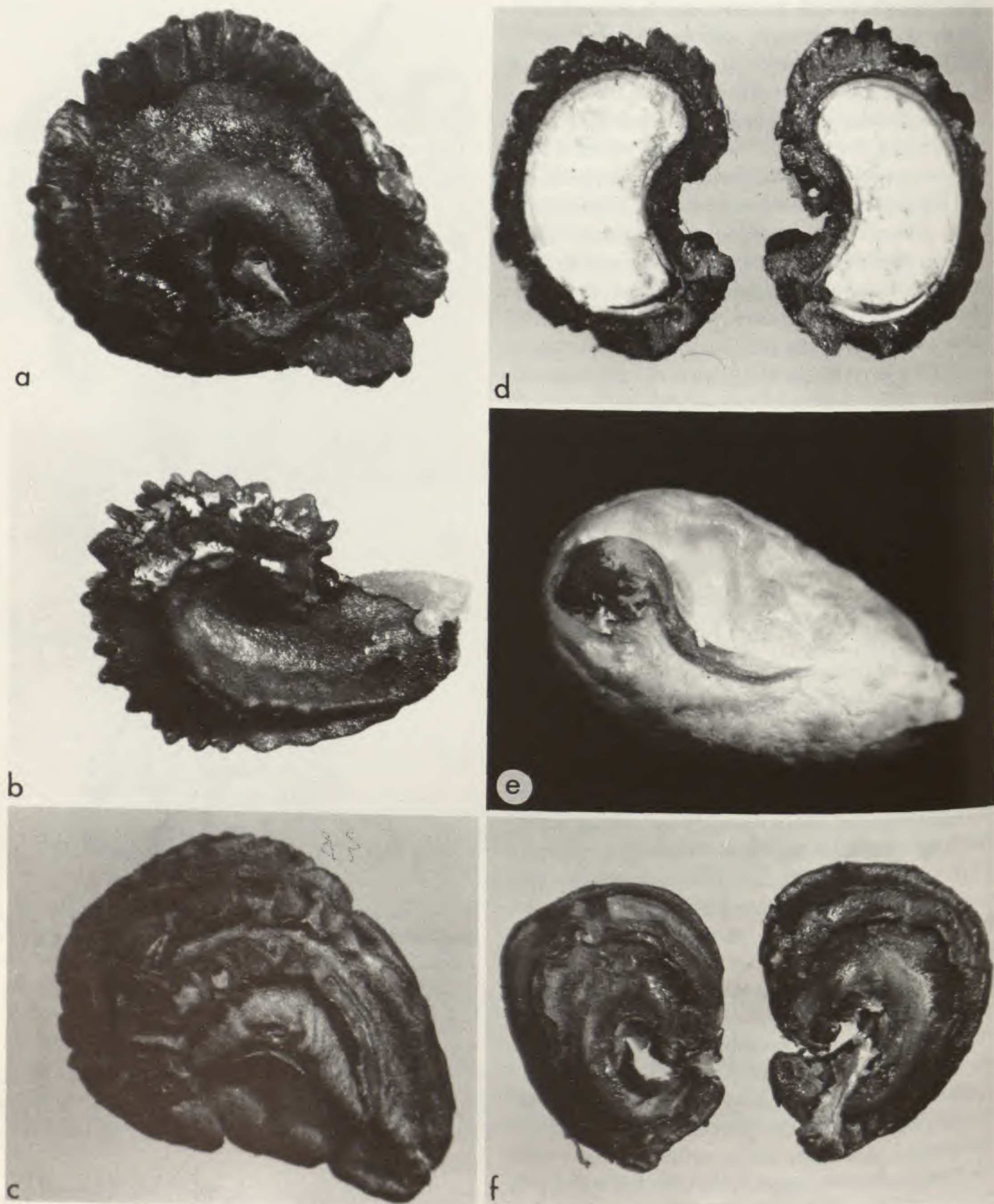


FIGURE 5. Seeds of Lasieae. —a. *Dracontium soconuscum* (Matuda 17783, UC). —b. *Dracontioides desciscens* (Harley et al. 2824, K). —c. *Anaphylloopsis cururuana* A. Hay (Anderson 10627, NY). —d. *Pycnospatha arietina* (Bogner 395, K). —e. *Anaphyllum wightii* (Hay s.n., FHO). —f. *Cyrtosperma merkusii* (Bogner 1363, K). See Figure 6 for scale.

recognition of *Dracontioides* as a relict descended from a caulescent “pre-Dracontium.”

**Anaphylloopsis** A. Hay, *Aroideana* 11(1): 25. 1988 and 11(2): 8. 1988. TYPE: *Anaphylloopsis*

*americana* (Engl.) A. Hay [Basionym: *Cyrtosperma americanum* Engl. in Martius, *Fl. Bras.* 3(2): 117, t. 22. 1878. Type: French Guiana: *Leprieur 152* (lectotype, P, selected by Hay, loc. cit., isoelectotype, US).]

Terrestrial or semiaquatic solitary herbs; rhizome erect, subterranean, bearing prophylls, cataphylls, and euphylls. Leaves solitary, rarely paired, with unarmed, usually warty petioles; lamina hastate to pinnate, dissected by fenestration and/or marginal outgrowth. Inflorescences solitary, rarely paired, on long peduncles similar to the petioles; spathe membranous, papery when dry, convolute in the lower part, otherwise spirally twisted; spadix with a stipe adnate for most of its length to the spathe. Flowers hermaphrodite throughout the spadix, with four tepals and four stamens; ovary unilocular, uni- to bi-ovulate with basal placentation; stigma wet. Fruit obpyramidal to ovoid, ripening reddish, with marcescent spathe. Seed campylotropous, pachychalazal, albuminous; coat thick, verruculose to deeply channeled; aril rudimentary, chalazal (Figs. 5c, 6c).

**Distribution.** Three species from tropical South America: *A. americana* from the Guianas, and two Amazonian species. Apparently all are rare, growing in swamp forest undergrowth, open swamps, riversides, and rainforest floor, at low altitude.

The genus is distinguished from *Dracontioides* by the spirally twisted as opposed to hood-forming spathe, solitary leaf, and unilocular ovary with basal placentation. It is distinguished from *Dracontium* by the rhizome, spathe, and posterior lobes of the leaf, which are never bifid or dichotomous. It is allied with these genera because of fenestration, cataphylls, tepals, and the ornate campylotropous seed.

The presence of both fenestrate and marginal leaf dissection within a single genus is matched by *Dracontium*.

SUBTRIBE 2. PYCNOSPETHINAE BOGNER

**Pycnospethinae** Bogner, Oesterr. Bot. Zeitschr. 122:202. 1973.

Cormous plants with solitary, usually highly dissected leaves. Spathe hood-forming. Flowers atepalate. Fruit spiny. Seed campylotropous, albuminous; seed coat hard, warty, containing druses.

**Distribution.** A single Indochinese genus.

**Pycnospetha** Thorel ex Gagnepain, Bull. Soc. Bot. France 88: 512. 1941. TYPE: *P. palmata* Thorel ex Gagnepain [Type: Laos: Ben-chom,

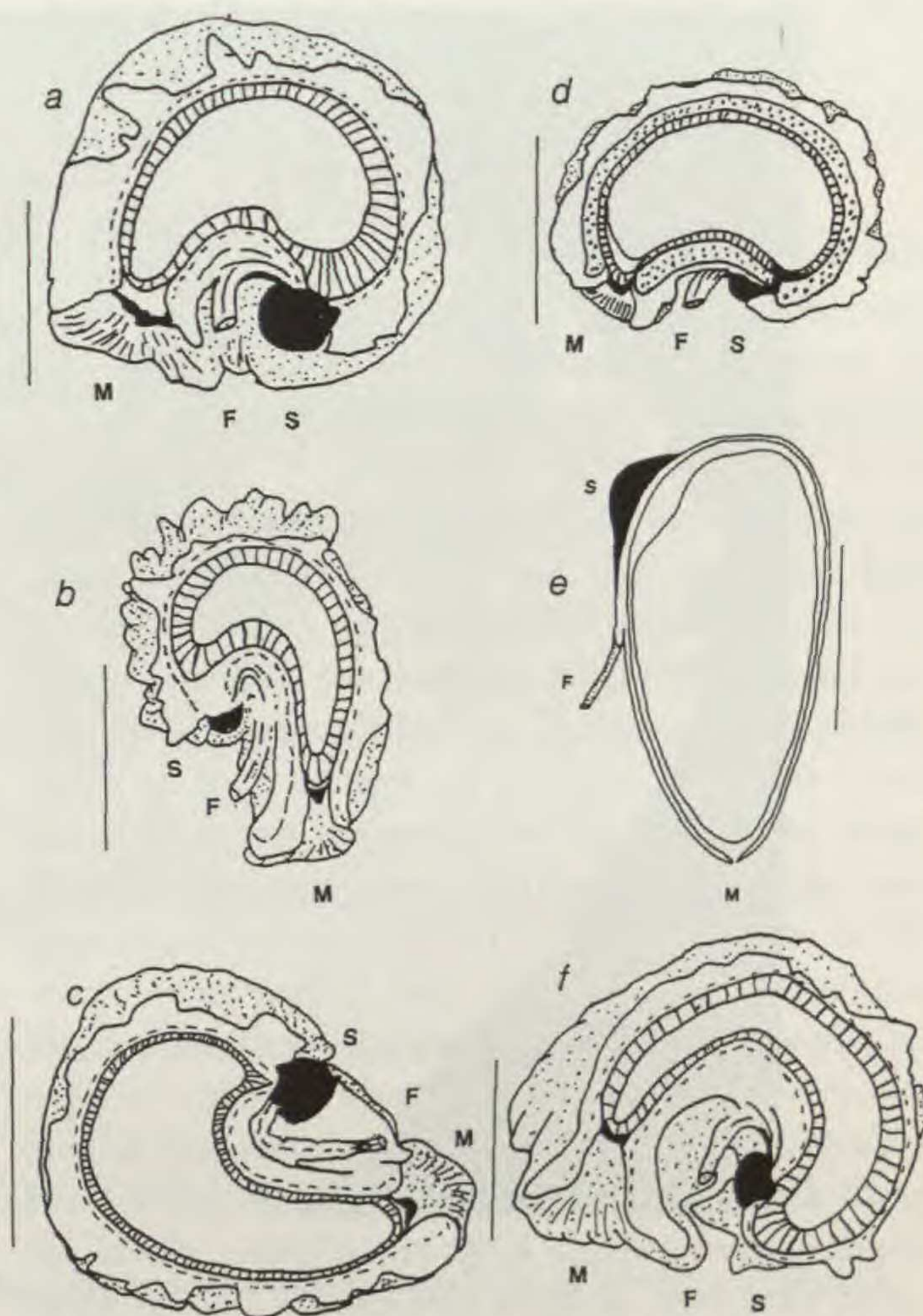


FIGURE 6. Seeds of Lasieae drawn from specimens in Figure 5.—a. *Dracontium soconuscum*.—b. *Dracontioides desciscens*.—c. *Anaphyllopsis cururuana*.—d. *Pycnospetha arietina*.—e. *Anaphyllum wightii*.—f. *Cyrtosperma merkusii*. F = funicle, M = micropyle, S = strophiole. Scale bar = 2 mm.

Sedom, Thorel 2404 (holotype, P).]

Cormous herbs with solitary highly dissected leaves on spiny spongy petioles, emerging from the cataphylls early as in *Dracontium* species; posterior lobes forked 3 times, anterior lobe trifold, the central member trifold again, the laterals unequally forked; leaflets sessile,  $\pm$  confluent, with brochidromous pinnate venation, or the leaf entire with the anterior lobe trisect with a pair of opposite lateral lobes, and the posterior lobes 1  $\times$  pedatifid; rachides with scattered leaflets throughout. Inflorescence solitary, accompanying the leaf, peduncle much shorter than the petiole; spathe sharply hood-forming, purple with pale longitudinal streaks; spadix sessile or shortly stipitate. Flowers hermaphrodite throughout, atepalate; stamens 6+; ovary unilocular, uniovulate with basal to subbasal placentation, style elongated, stigma punctiform. Fruit a reddish spiny berry ca. 1 cm diam. (Fig. 7), pericarp (in spirit material) hard, rather corky,



FIGURE 7. Pericarp of *Pycnospatha arietina* (Bogner 395, K). The fruit is ca. 1 cm in diameter.

firmly appressed around the seed. Seed black or very dark brown, seed coat hard, thick, warty, containing white druses in "tegmic" layer of pachychalaza (Figs. 5d, 6d).

*Distribution.* Two species from rather open sites in areas of evergreen forest in Thailand and Laos. Rare. Bogner (pers. comm.) noted that *P. arietina* Thorel ex Gagnepain is locally common in Thailand.

The genus has recently been revised and the species described in detail by Bogner (1973). He recognized two species, reducing *P. soerensenii* S. Y. Hu to synonymy with *P. arietina*. Bogner noted that the genus is close to *Dracontium* on the basis of the corm, highly compound  $\pm$  solitary leaves, spiny petioles, hooded spathe, and warty seed coat, a conclusion with which I concur. However, the presence of druses in the seed coat, which are unknown in other members of the Lasieae, and the atepalate flowers set the genus apart.

The leaf blade of *P. arietina* is similar to that of some species of *Dracontium*, but at no stage in the juvenile to adult sequence is there any evidence of fenestrate development, hence the segments may be regarded as outgrowths rather than as "cut-outs." The posterior rachides are more or less equally divided three times, with the outermost (i.e.,

those farthest from the anterior lobe) products of each fork somewhat more elaborate than the inner, creating a "tri-pedate" effect. The anterior rachis undergoes a major division into three about a third of the way along its length, and the central member repeats this near the tip. The lateral members of these divisions undergo somewhat irregular forking with some overtopping. Throughout, the rachides are bounded by an irregular narrow wing arising on the adaxial surface on either side of the lamina. Here and there, this wing is thrown into a "leaflet," the costa(e) of which emerge(s) from the adaxial part of the rachis. By contrast, the major divisions of the rachides are complete and more or less equal, including those that produce the ultimate rachillae. Those leaflets that are scattered along the main rachides may be regarded as supernumerary, and their origin is tentatively ascribed to a process of space filling in the tightly folded developing leaf. They also occur in species of *Amorphophallus*, *Dracontium*, and *Taccarum*, and in *Tacca leontopetaloides* (L.) Kuntze (Taccaceae). The leaf construction of the last-mentioned is very similar to that of *Pycnospatha arietina*.

In subadult leaves of *P. arietina*, the anterior lobe is trilobed with two pairs of opposite costae corresponding to the divisions of the mature anterior rachis described above. The posterior lobes

are bilobed, with their midribs forked. Adult leaves of *P. palmata* are almost identical with subadult leaves of *P. arietina*, and the species seem otherwise to differ only in the style, which is straight in *P. arietina* and curved in *P. palmata*.

The Monstereae have a preponderance of members with naked hermaphrodite flowers; otherwise, only *Calla* of the enigmatic Calloideae shares this characteristic with *Pycnospatha*. Indeed, Gagnepain (1941) stated that *Pycnospatha* clearly belongs in the Calloideae, although he indicated that the spadix contains a mix of male and female flowers. This was not Krause's view of *Calla*, for which he noted "flores hermaphroditi vel superiores abortu masculi, nudi" (Krause, 1908). Bogner (1973) took the view, followed here, that the flowers of *Pycnospatha* are hermaphrodite.

Spiny fruits are extremely rare in the Araceae, occurring only in this genus and in *Lasia*. In both genera the spines are rudimentary and scarcely seem to have ecological significance. The phylogenetic significance of spiny fruits has been discussed by Corner (1949, 1952-1954, 1964, 1966) in relation to the Durian Theory. The allegedly primitive armed loculicidal capsule of arillate seeds is not known to occur in Araceae, although arillate seeds are known and sarcotestas are common. In the Lasieae the seed has an oily strophiole and the fruits are indeshiscent. That spines appear in a more or less rudimentary state in this relictual group suggests that they may be interpreted as vestigial.

The seed is less strongly curved in *Pycnospatha* than in other members of the tribe (other than *Anaphyllum*), has a slightly enlarged hilum, and its coat is dark brown throughout, whereas in other genera the pigmentation is concentrated in the surface layers of cells. The inclusion of white crystalline druses is unique.

#### SUBTRIBE 3. ANAPHYLLINAE

Subtribe **Anaphyllinae** A. Hay, subtribe nov.

TYPE: *Anaphyllum* Schott.

Caudex hypogaeus, rhizomatosus, sobolifer vel stolonifer, cataphyllis, prophyllis euphyllisque praeditus; foliorum lamina pinnata vel pinnatipartita, haud fenestrata; spathe spiraliter torta vel plusminusve plana; flores tetrameri; semen anatropum, ovoideum, laeve; integumentum tenue, membranaceum; embryo crassus, rectus; albumen nullum.

*Distribution.* A single genus, *Anaphyllum*, restricted to southern India.

**Anaphyllum** Schott, Gen. Aroid. t. 83. 1858.

TYPE: *Anaphyllum wightii* Schott [Type: India. Karnataka: Courtallum, *Wight* 2776 (holotype, K).]

Clump- or colony-forming herbs; stem a sympodial series of rhizomes bearing prophylls, cataphylls, and a few foliage leaves. Petioles to ca. 1.5 m tall, smooth to tubercular and then sometimes with warts on distinctly raised flanges, rarely (?) armed; blade pinnate with opposite leaflets, the terminal segment trifid and the posterior lobes sometimes bifid, or the leaf pinnatisect; rachis with a geniculum at the junction with the first and second leaflet pairs, or only at the apex of the petiole. Inflorescence solitary, on a peduncle similar to and about equaling the petiole in length; spathe membranous to coriaceous, marcescent, basally convolute and spirally twisted in the remainder, or the whole ovate and  $\pm$  flat; spadix much shorter than the spathe, free-stipitate. Flowers tetramerous; receptive stigmas with pollination droplets; ovary unilocular and uniovulate, with parietal placentation. Fruit ovoid, smooth, ripening red. Seed ovoid, filling the locule, anatropous, on a slender funicle thickening toward attachment to seed; seed coat unlig-nified, membranous, smooth; endosperm absent; embryo stout, straight (Figs. 5e, 6e).

*Distribution.* Two species from southern India, in evergreen forest and swamp forest undergrowth.

Sivadasan (ined.) recognized three infraspecific taxa in *A. wightii*. The second species, *A. beddomei* Engl., is distinguished by its ovate, open spathe and pinnatifid leaves in contrast to the twisted convolute spathe and usually pinnate leaves of *A. wightii*.

The genus is remarkable for its soft and membranous seed coats, in contrast to the hard ornate campylotropous seeds of other members of the tribe. Monosulcate pollen, early emergence of the leaves, and basipetal maturation of the spadix, however, mark the genus as belonging in the Lasieae.

#### SUBTRIBE 4. LASIINAE SCHOTT

**Lasiinae** Schott, Prodr. Aroid. 399. 1860. "Lasiinae."

Rhizomatous or suffruticose, solitary, clump-forming, or colonial herbs; leaves and more rarely stems usually armed, sometimes heavily; modules of sympodia multifoliar, with prophylls and euphylls only; leaf blades simple, dissected to hastate;

inflorescence solitary, rarely cymose-paired, on peduncles similar to the petioles; spathes erect to deflected, very rarely hood-forming, sometimes acuminate-twisted, persistent, marcescent, or caducous. Flowers 6-(5-)4-tepalate and -staminate; filaments free, rarely united; ovary bi- or unilocular, multi- to uniovulate; placentation axile, basal, parietal or apical. Fruit a green to red, spiny to smooth, 1-several-seeded berry. Seed campylotropous, reniform, rarely helical, albuminous or not; seed coat hard, pachychalazal, often warty or crested, sometimes smooth.

*Distribution.* Pantropical excluding Australia. Five genera.

#### KEY TO GENERA

- 1a. Stems suffruticose, erect to decumbent, usually with spiny internodes, rarely a condensed rhizome; leaves usually dissected, or hastate; spathe caducous or rarely marcescent; placentation apical; fruit usually spiny. Indomalesia ..... *Lasia*
- 1b. Stem usually a condensed rhizome, rarely with distinct internodes and then unarmed; leaves entire, sagittate to hastate or lanceolate; spathe persistent to marcescent; placentation otherwise; fruit smooth.
- 2a. Plants always unarmed; ovary bilocular or rarely unilocular; seed mostly exalbuminous; petioles soft and spongy in the dry state. Neotropics ..... *Urospatha*
- 2b. Plants nearly always armed (some individuals unarmed); ovary unilocular; seed albuminous or exalbuminous; petioles usually drying rigid. Paleotropics.
- 3a. Petioles angular in cross section, armed in rows along the edges; plants stoloniferous, forming large colonies; spathe persistent; filaments of stamens united. Africa ..... *Lasiomorpha*
- 3b. Petioles  $\pm$  terete in cross section; armature scattered or in oblique combs; plants solitary or forming small clumps; spathe marcescent or persistent; filaments of stamens free.
- 4a. Spines straight and turned downward; rhizome with distinct internodes and roots emerging from between the persistent leaf bases; seed smooth,  $\pm$  orbicular, to 7 mm diam. West Malesia ... *Podolasia*
- 4b. Spines straight and upturned; rhizome condensed; seed crested and/or warty, if smooth then less than 5 mm diam. Malesia to Oceania ..... *Cyrtosperma*

An argument could be made for reducing all the genera of the Lasiinae to *Lasia*. The generic limits are narrow. However, the groups here circumscribed appear natural on morphological, geo-

graphical, and ecological grounds, and rather than making a large number of new combinations, I have resurrected *Lasiomorpha* to maintain the status quo. The Old World genera have recently been revised by Hay (1988a).

**Cyrtosperma** Griff., Notul. 3: 149. 1851 & Icon. Pl. Asiat. t. 169. 1851. TYPE: *C. lasioides* Griff. [Type: Malaysia: Malacca, Griffith 5059 (holotype, K).] = *C. merkusii* (Hassk.) Schott.

*Arisacontis* Schott, Bonplandia 5: 129. 1857. TYPE: *A. chamissonis* Schott (= *C. merkusii*).

[*Apereoa* Moerenhout, Voyages aux Îles du Grand Ocean 2: 16. 1837, nom. nud.]

Massive to slender rhizomatous herbs, usually solitary, occasionally clump-forming; rhizome thick, condensed, creeping, the older parts long-persistent or quickly rotting. Leaves several, on spiny petioles to ca. 3 m long; blades hastate to sagittate, with a prominent geniculum at apex of petiole. Inflorescence solitary, rarely paired, on peduncles similar to the petioles; spathe erect, rarely somewhat hood-forming, occasionally with the upper part long-acuminate and twisted, convolute or not in the lower part, blackish purple to white; spadix sessile to stipitate. Flowers 6-(5-)4-tepalate and -staminate; filaments free; receptive stigmas wet; ovary unilocular, multi- or uniovulate; placentation basal or parietal. Seed strongly campylotropous, reniform to orbicular to helically twisted, pachychalazal, crested, warty or smooth, albuminous (Figs. 5f, 6f).

*Distribution.* Eleven species: *C. merkusii* from the Malay Peninsula, Borneo, Sumatra, Java, the Philippines, and Oceania, the rest Papuan. None is recorded from Sulawesi, Halmahera, or Australia.

*Cyrtosperma giganteum* Engl. has multiovulate locules. The remaining species are bi- or uniovulate. In part of its range, which has apparently been greatly extended by humans, *C. merkusii* (syn. *C. chamissonis* (Schott) Merr., *C. edule* Schott) is cultivated for the edible and sometimes huge (to ca. 60 kg) rhizome. *Cyrtosperma johnstonii* (Bull) N. E. Br. is cultivated as an ornamental, and there are no wild collections of it, apart perhaps from a seedling from Buka Island in the Papua New Guinea Solomon Islands. *Cyrtosperma cuspidispathum* Alderw. is remarkable for its huge size (the leaves may reach 4 m in length) and for its fruits, which are expelled from the spadix at maturity and remain attached to it by the inner

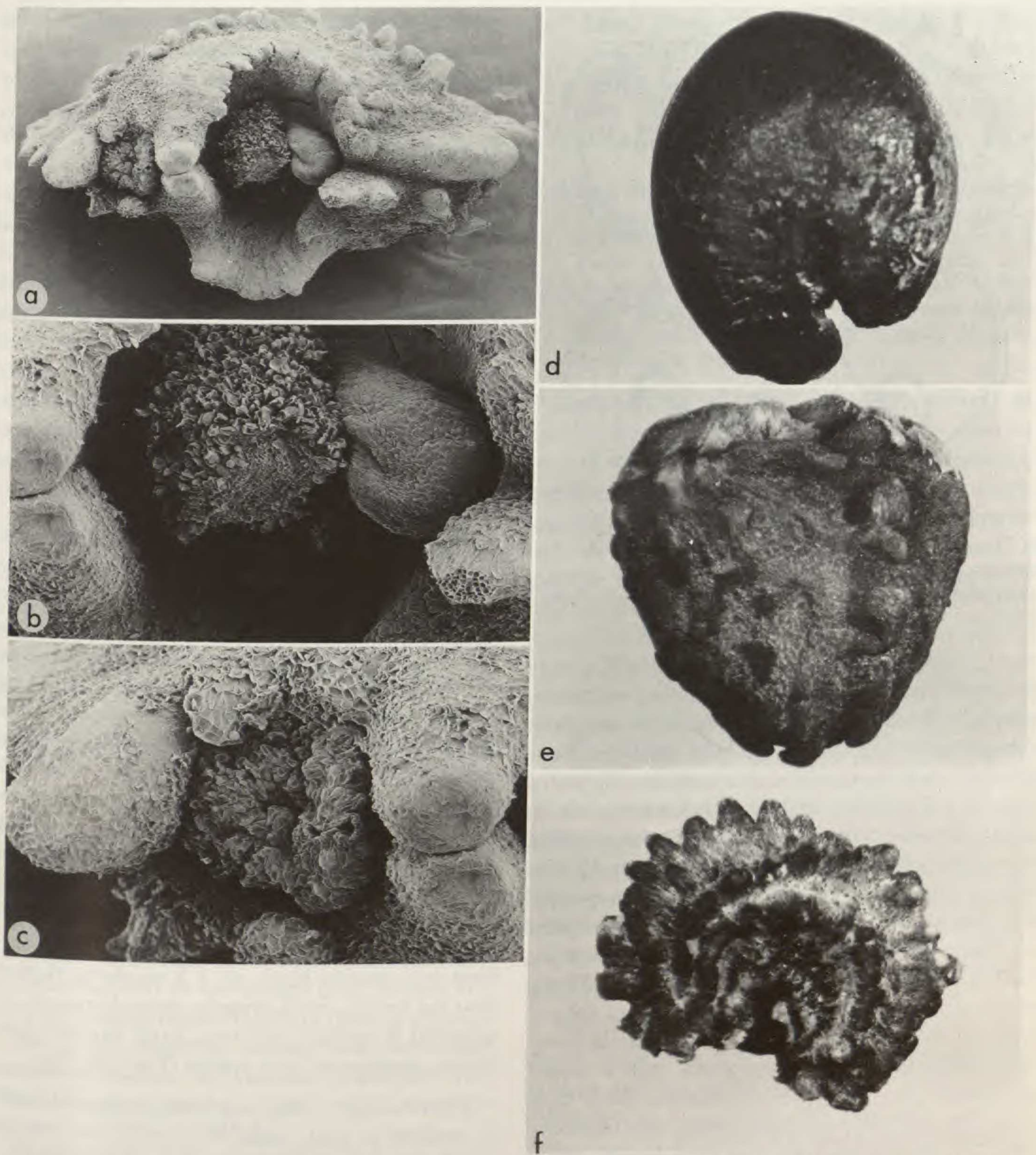


FIGURE 8. Seeds of Lasieae.—a-c. SEM of *Lasiomorpha senegalensis* (Hay 2701, FHO).—a. Ventral view.—b. Detail of funicle and strophiole: the locule is filled with mucilage, which may be secreted by the glandular cells covering the funicle.—c. Micropyle: note the operculum with collapsed ovular micropyle. The seed coat appears to be the result of growth in the chalazal region of the ovule. It forms a “new” coat and a “new” micropyle and throws the ovular integuments forward as an operculum. The pattern is typical of all genera except *Anaphyllum*.—d. *Podolasia stipitata* (King’s collector 5324, K).—e. *Lasia spinosa* (Nicolson 1651, K).—f. *Urospatha sagittifolia* (Bogner 580, K). See Figure 9 for scale.

epidermis of the tepals, as is often the case in *Anthurium* (Hay, 1988a, 1990).

**Lasiomorpha** Schott, Bonplandia 5: 127. 1857.  
TYPE: *Lasiomorpha senegalensis* Schott (syn. *Cyrtosperma senegalense* (Schott) Engl.).

[Type: Senegal: Perrotet 763 (lectotype, P, selected by Knecht, 1983).]

Robust and sometimes massive colony-forming herb to 3.5 m high; stem a short dense rhizome to 12 cm diam. bearing slender, sometimes branching stolons to 3 m long. Leaves several together,

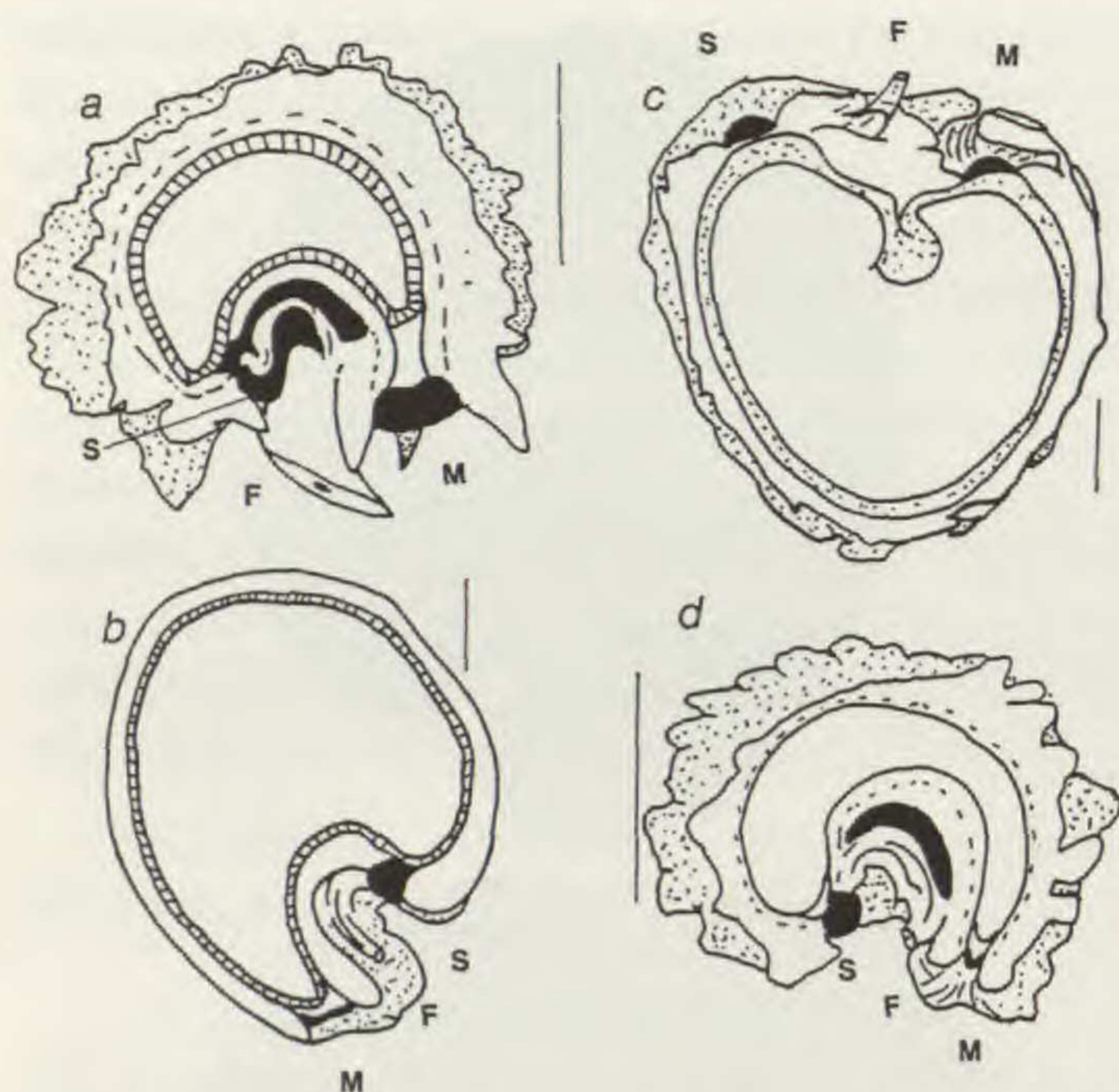


FIGURE 9. Seeds of Lasieae drawn from specimens in Figure 8.—a. *Lasiomorpha senegalensis*.—b. *Podolasia stipitata*.—c. *Lasia spinosa*.—d. *Urospatha sagittifolia*. F = funicle, M = micropyle, S = strophiole. Scale bar = 2 mm.

on petioles angular in cross section and armed in vertical rows along the edges; sheath short, persistent; geniculum absent or very weakly differentiated; blade hastate to sagittate, unarmed, leathery, to 1.2 m long. Inflorescence solitary on a peduncle similar to and about equaling the petioles, without a geniculum; spathe ovate, to ca. 40 cm long, convolute in the lower portion, erect, brownish green without, purple streaked with yellow within, after anthesis becoming green, persistent; spadix shorter than the spathe,  $\pm$  sessile. Flowers 4-tepalate and -staminate; filaments united into a short tube; ovary slightly inferior; pollination drops present; ovary unilocular, 4–6-ovulate, with a rather prominent basal and parietal placenta. Seeds to 5  $\times$  5 mm, strongly campylotropous, with rudimentary aril, several per fruit; coat hard, brown, warty and spiny (Figs. 8a, b, c, 9a).

**Distribution.** A single Tropical West African species from Senegal to Chad to Angola, in ditches, swamps, ponds, and swamp-forest gaps; often very common.

Engler (1879, 1911) included *Lasiomorpha senegalensis* and *Cyrtosperma giganteum* in his section *Lasiomorpha* of *Cyrtosperma* because of the multiovulate, unilocular ovary, and endospermous seed. *Lasiomorpha senegalensis* differs from *Cyrtosperma* sensu stricto by having persistent spathes (a feature shared with *Urospatha*), angular petioles (similar to the unarmed ones of *Urospatha*

*loefgreniana* Engl.), stolons (occurring otherwise only in *Lasia*), more elaborate fruits with tough red inner and outer epidermis and white mesocarp, filaments united into a tube (a previously overlooked feature), somewhat inferior ovaries, and absence of (or weakly differentiated) genicula on the petioles and peduncles. These distinguishing characters are matched by its isolated geographical position (Hay, 1988a).

Schott recognized a second species, *L. afzelii*, based on a monstrosity with a  $\pm$  spherical spadix (Brown, 1902).

**Podolasia** N. E. Br., Gard. Chron. New Ser. 18(2): 70. 1882. TYPE: *P. stipitata* N. E. Br. [Type: cult. in Hort. Veitch ex Borneo, Curtis s.n. (holotype, K).]

Rhizomatous herbs, solitary or forming small clumps by branching of the rhizome; stem erect to decumbent, short, to ca. 2.5 cm diam., with distinct, unarmed, green internodes to ca. 2 cm long, rooting between the persistent leaf bases. Leaves several together, hastate to sagittate, with long petioles armed with mostly down-pointing, stout spines. Inflorescence solitary; peduncle similar to and about equaling the petioles; spathe ovate-lanceolate, purple-brown, open to the base; spadix usually stipitate, the stipe growing considerably after the spathe has opened. Flowers hermaphrodite throughout, 4–6-tepalate and staminate; filaments free; ovary unilocular, uniovulate with parietal to basal placentation; receptive stigmas wet. Fruit red, smooth, large, ca. 1.2 cm diam., thicker than the spadix. Seed strongly campylotropous,  $\pm$  spherical in outline; coat thin, hard, smooth, dark brown; endosperm very sparse (Figs. 8d, 9b).

**Distribution.** One west Malesian species chiefly confined to peaty soils.

The genus appears intermediate between *Cyrtosperma* and *Lasia* in its photosynthetic, rather elongated stem and in the venation of the posterior lobes, which is more similar to that of hastate leaves of *Lasia spinosa* than it is to *Cyrtosperma*. *Podolasia* agrees with *Cyrtosperma* in placentation and fruit.

*Podolasia stipitata* was introduced from Borneo by the nurseryman Veitch and described from cultivated material.

**Lasia** Lour., Fl. Cochinch. 81. 1790. Not "*Lasia*" P. Beauv. (1804), which is *Forsstroemia* Lindberg (Musci—Cryphaeaceae). TYPE of *Lasia*:

*L. aculeata* Lour. [Type: Vietnam, nr. Hanoi, Loureiro s.n. (holotype, BM).] = *L. spinosa* (L.) Thwaites.

[*Lasius* Hassk., Cat. Bog. 59. 1844. sphalm.]

Clump and colony-forming (rhizomatous or) suffruticose stoloniferous herbs; stems orthotropic to decumbent, to ca. 1.5 m long/tall, with distinct prickly green internodes (or condensed and unarmed). Leaves several; petioles prickly, drying spongy, not or faintly mottled; blades (4×-)pinnatifid to hastate. Inflorescence solitary, on peduncles similar to and usually shorter than the petioles; spathe narrowly lanceolate (rarely ovate), convolute at base often long acuminate and spirally twisted, caducous (or marcescent), purplish brown to greenish; insertion annular, not oblique; spadix sessile. Flowers 4(-6)-tepale and -staminate; filaments free; ovary unilocular, uniovulate, with apical placentation. Fruit green, minutely spiny in apical part or spines absent. Seed large, ± pyramidal, ca. 1 cm diam., seed coat thin, brown, hard, with a few appressed spines; endosperm absent (or residual) (Figs. 8e, 9c).

*Distribution.* The full range of the genus is occupied by *L. spinosa* (L.) Thwaites, from India and Sri Lanka to Nepal, China, Indochina, and Malesia; not recorded from Sulawesi, Moluccas, or Australia; in moist forests and open swamps and ditches, to 350 m.

A second species is known only from cultivation: *Lasia concinna* Alderw. was described from a single individual said to have come from Borneo and is still growing at Bogor. It differs from *L. spinosa* in the 3-4× dissected leaves, ovate-lanceolate marcescent spathe, and massive condensed rhizome. This plant may be a hybrid with *Cyrtosperma merkusii* (Hay, 1988c).

In spite of the wide range of *L. spinosa*, there is no obvious dispersal mechanism. The fruits remain green, and though spiny in their top part, there is no tendency to form hooks; in some individuals spines are lacking. Apparently the infructescences disintegrate, and the fruits get washed along. It is therefore of interest that *Lasia* occurs on both sides of Wallace's Line and is absent from Sulawesi. The seeds and fruits show no apparent adaptation to enable them to survive long inundation in salt water. Geography of the Lasiinae is discussed at the end of this paper.

*Urospatha* Schott, Aroideae 3, figs. 8-10. 1853 & Gen. Aroid. 86. 1858. LECTOTYPE: *U. sagit-*

*tifolia* (Rudge) Schott, selected by Nicolson (1967). [Basionym: *Pothos sagittifolium* Rudge, Pl. Gui. 24, t. 34. 1805. Type: "Guiana," Martin s.n. in Herb. Rudge (holotype, BM).]

*Urospathella* Bunting, Phytologia 65: 391. 1988. TYPE: *Urospathella wurdackii* (Bunting) Bunting. [Basionym: *Cyrtosperma wurdackii* Bunting, Acta Bot. Venez. 10: 285. 1975 [1977] = *Urospatha wurdackii* (Bunting) A. Hay, Blumea 33: 457. 1988. Type: Venezuela. Territorio Federal Amazonas: Río Guainía, sabanita, 1 km above Pimichín, Maguire & Wurdack 36384 (holotype, NY).]

Unarmed herbs, robust to slender, solitary or clump-forming, with condensed rhizomes. Leaves several together, on smooth to rough, sometimes angular petioles; blades sagittate, hastate, sometimes lanceolate with the posterior lobes absent or reduced to auricles; venation of the anterior lobe pinnate or curvined (when the anterior lobe much reduced and slender, then the primary veins reduced to 2 submarginal veins and the secondaries pinnately arranged along the midrib). Inflorescence solitary on peduncles similar to the petioles; spathe erect, usually convolute in lower part, mostly with a twisted acuminate upper portion, sometimes ± flat; spadix with hermaphrodite flowers throughout, sessile or stipitate. Flowers 4-6-tepalate and -staminate; filaments free; ovary usually bilocular with axile placentation or unilocular with basal-parietal placentation; receptive stigmas wet. Seed campylotropous, smooth to heavily warted, pachychalazal; seed coat hard, brown; endosperm usually absent (Figs. 8f, 9d).

*Distribution.* About twelve species from Central America and tropical South America, mostly in open habitats including wet places in savanna vegetation.

The genus is in need of revision. It is apparently one of the larger genera of Lasieae. However, a number of the "species" may be referable to *U. sagittifolia* in addition to those already suggested for merging by Jonker-Verhoef & Jonker (1953). The "species" seem to be rather characterless in the herbarium, and more photographs and living material would prove useful. For example, the angular petioles of *U. loefgreniana* Engler, from Brazil, become more or less indistinguishable from cylindrical petioles when dried. Leaf shape and venation are extremely variable within species of *Cyrtosperma*, *Lasia*, *Lasiomorpha*, and *Podolasia*. No doubt this is the case in this genus. Likewise it is highly probable that flowering takes place



before the plants have reached full size, so that the inflorescences can be expected to be phenotypically variable as well. Seeds may prove to be useful in species delimitation.

This genus and *Dracontium* show the parallel reduction series to the unilocular condition already completed in other genera. Since Engler's monograph (1911), in which he considered *Urospatha* characteristically to have bilocular ovaries, two Venezuelan species with unilocular ovaries have been described: *U. savannarum* Steyermark and *U. wurdackii* (Bunting) A. Hay. The latter was first described as a species of *Cyrtosperma* (see above). Bunting (1988) recently erected the genus *Urospathella* for the latter species, giving no adequate grounds for not recognizing the species in *Urospatha*. He argued that the unilocular ovary sets it aside from *Urospatha* sensu stricto and took the stance that the unilocular ovary described for *Urospatha savannarum* Steyermark is yet to be verified. However, Steyermark showed in his figure of *Urospatha savannarum* a unilocular ovary (Steyermark, 1951, fig. 15). In his diagnosis of *Urospathella* Bunting (1988) described the locule as bilovulate, as it often is in bilocular species of *Urospatha*. He noted that the ovules are basifixed, where they are centrally placed on the partition of the ovary in the bilocular species. Clearly in unilocular species the ovules cannot occupy the position they occupy in the bilocular species, so that in this case the position of the ovules can carry very little weight. He also reported that the ovule form is also distinctive "having the funiculus inserted at the center of the ovule, nearly perpendicular to its axis." If it is to be understood from this that the funicle is inserted about midway along the length of the ovule, this is normal for the tribe.

He further distinguished *Urospathella* from *Urospatha* on the basis of the twisted spathe of the latter. The spathe is not twisted in *Urospatha savannarum* (Bogner, pers. comm.), and species with twisted and untwisted spathes occur in *Lasia*, *Cyrtosperma*, and *Anaphyllum*. This distinction in spathe form concerns only the distal portion of the spathe limb and is trivial compared with distinctions in spathe form affecting the body of the spathe, such as between *Dracontioides* and *Anaphyllopsis*.

Bunting (1988) further reported seed form and leaf shape as distinguishing features of *Urospathella*. Verrucose exalbuminous seeds occur in *Urospatha wurdackii* and in other species of *Urospatha* (Bogner, pers. comm., see also Figs. 8f and 9d). More recently, Bunting (1989) has published

anatomical evidence that the seed of "*Urospathella wurdackii*" is albuminous, supporting the segregation of this species in a genus of its own. However, it now seems that the status of the endosperm in mature seeds of *Urospatha* species is something of a gray area, with small amounts of endosperm sometimes being found in the seeds of *U. sagittifolia* (Bogner, pers. comm.). In effect, this finding removes the only reason for segregating *Urospathella* that carries significant weight. The lanceolate leaf is a distinctive feature of this species, and, in Bunting's (1988, 1989) view, of the genus *Urospathella*. The seedling leaves of *Urospatha sagittifolia* are ovate to lanceolate (Bogner, pers. comm.) as they are in *Cyrtosperma*. A putative case of neoteny in the foliage leaf blade is an inadequate basis for a genus, especially in a family where diversity of leaf form characterizes so many genera. Even taken together, the suite of characters Bunting used to erect *Urospathella* can only be seen as those distinguishing "*Urospathella wurdackii*" from other species of *Urospatha*.

The Englerian concept of *Urospatha* (bilocular ovaries; exalbuminous seeds) is no longer tenable. At this point it remains only to say that *Urospatha* sens. lat. seems homogeneous in both aspect and geography, but that it requires a monograph for its characterization to be established.

*Urospatha friedrichsthalii* Schott, from Nicaragua, an illustration of which accompanies the generic protologue (Schott, 1853, fig. 7), is a *Sagittaria* (possibly *S. montevidensis* Cham. & Schlecht.) in the Alismataceae.

#### GEOGRAPHY OF THE TRIBE

In the absence of fossil evidence earlier than the Miocene for seeds attributed to *Urospatha* from Germany and the Urals (Mai & Gregor, 1982; Gregor & Bogner, 1984), interpretation of the distribution of the Lasieae with reference to their age and origin is problematic. Distributions of the tribe and the subtribes are shown in Figures 10-13.

The distribution of the Dracontiinae (Fig. 10) suggests that this group is Gondwanan in origin and that *Dracontium* has extended northward into Central America and southern North America. *Anaphyllopsis* and *Dracontioides* have relict distributions in South America and are confined to areas coinciding exactly with Pleistocene forest refugia proposed by Prance (1982). *Anaphyllopsis* has three species confined one to each of three refugia in the Guianas, western Venezuela, and Pará, Brazil

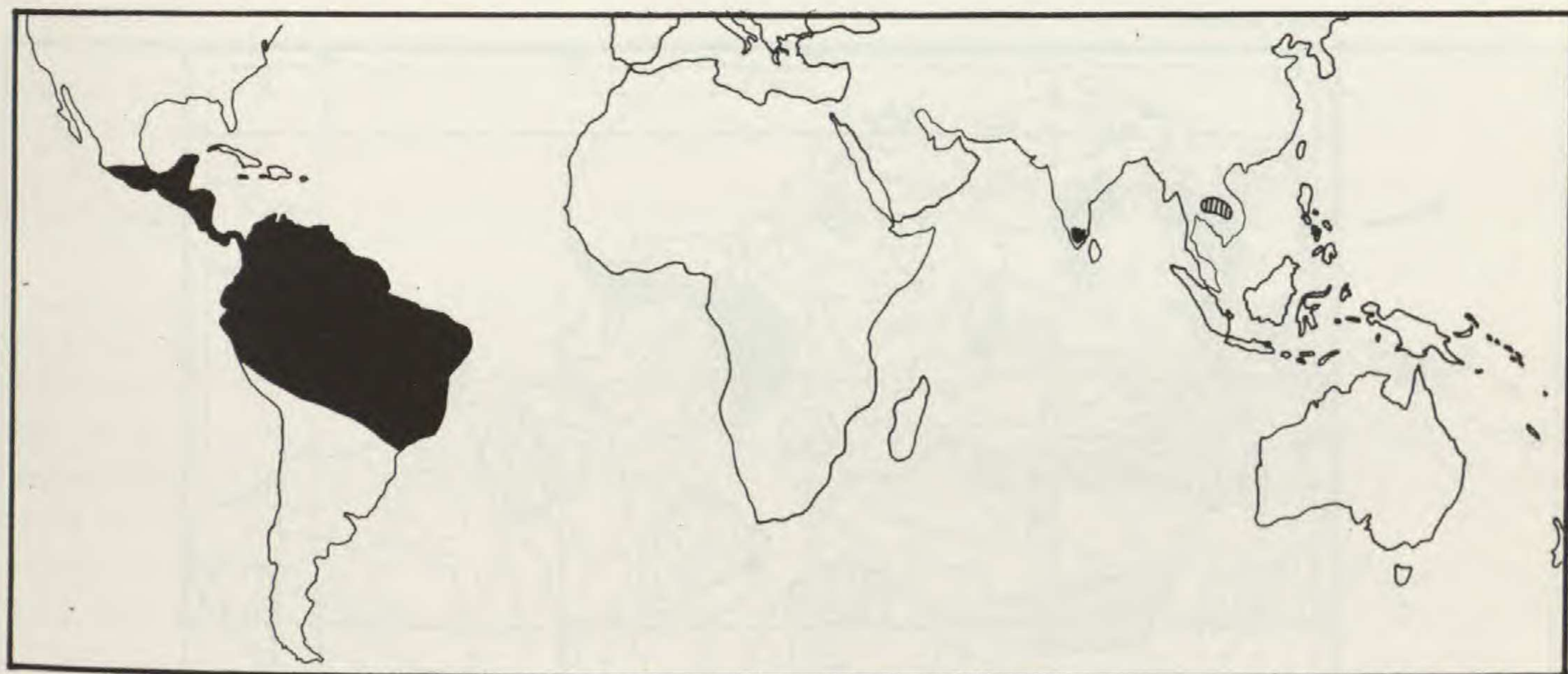


FIGURE 10. World distribution of Lasieae subtribes Dracontiinae (black, New World), Anaphyllinae (black, India), and Pycnospathinae (vertical hatching).

(Hay, 1988b) and the monotypic *Dracontioides* is confined to two refugia in eastern Brazil (Fig. 11). By contrast, Pycnospathinae (Fig. 10), considered here and by Bogner (1973) to be closest to Dracontiinae, are isolated relictually in Laurasian Indochina. Anaphyllinae (Fig. 10) are restricted to and relictual in Gondwanan India, though one cannot discount the possibility of *Anaphyllum* having migrated into India from a Tertiary tropical Laurasian flora such as postulated by Wolfe (1975).

The Lasiinae (Fig. 12), whose distribution almost covers that of the whole tribe, are similarly equivocal. *Lasiomorpha* and *Urospatha* show close austral amphi-Atlantic affinity, suggesting Gondwanan origin. However, in the East (Fig. 13), there is a center of generic diversity in Laurasian West Malesia (one species each of *Lasia*, *Podolasia*, and *Cyrtosperma*), and *Lasia spinosa* and eleven species of *Cyrtosperma* in Gondwanan Papuasias, with no representatives in Sulawesi, Halmahera, or Australia.

The Papuasian representatives of *Cyrtosperma* are almost certainly originally Papuasian. The species are few, uncommon, and mostly well differentiated at specific and supraspecific levels, and thus the genus does not appear to be a new arrival undergoing speciation. However, *Cyrtosperma merkusii*, which is evidently wild only west of Wallace's Line, a biogeographic demarcation reflecting a line of contact between the Australian plate and Laurasia, has its closest relatives in the Solomon Islands and the Lousiade Archipelago, except for *C. giganteum*, which is known only from a single locality on the New Guinea mainland. It can be suggested that, since the collision of the Australian

plate with the Indonesian Archipelago some 15 million years ago (Whitmore, 1973), a *Cyrtosperma* crossed Wallace's Line and *C. merkusii* subsequently evolved in West Malesia. However, the absence of the genus from Sulawesi and Halmahera, and the confinement of most of the nearest relatives of *C. merkusii* to eastern Papuasias militate against this suggestion. Furthermore, although *Cyrtosperma* is probably bird-dispersed, there are no species common to long-separated islands (except in the eastern part of the range of *C. merkusii*, where human agency is suspected), indicating that migration across open ocean is highly improbable.

A similar though reversed picture is presented by *Lasia spinosa*. (The second species of *Lasia*, *L. concinna*, is of doubtful status and origin and is ignored here.) *Lasia spinosa* is found from Sri Lanka to southern China and West Malesia, where it is restricted to areas bounded by the Sunda Shelf. It is absent from the Philippines, Sulawesi, and Halmahera, and then reappears on the Sahul Shelf as a rare plant throughout lowland New Guinea and in the Bismarck Archipelago (Hay, 1981, 1988a), though it is absent from Australia. It has no evident means of traversing open ocean: the fruit wall is thin, fleshy, unpalatable, and inconspicuous; though minutely thorny, it is not hooked or sticky. The seed coat, although hard, is thin and the micropyle is large; neither the seed nor the fruit seem likely to survive more than a short period of inundation in salt water. *Lasia spinosa* is a freshwater swamp plant occurring mostly in open habitats in seasonal and aseasonal climates. If *Cyrtosperma*, *Lasiomorpha*, and *Urospatha* originated in Gondwanaland, it seems reasonable to



FIGURE 11. The distribution of *Anaphyllopsis* and *Dracontioides* species mapped over Prance's (1982) proposed Pleistocene refugia in South America. ▲ = *Anaphyllopsis cururuana*. △ = *Anaphyllopsis americana*. ◆ = *Anaphyllopsis pinnata* A. Hay. ● = *Dracontioides desciscens*.

surmise that *Lasia* did also, and that it was rafted on India and migrated through Southeast Asia after India reached its present position in the late Tertiary (Axelrod, 1970). However, it is difficult to envisage its migration to New Guinea, both for the morphological reasons above, and on account of its absence from Philippines, Sulawesi, and Halmahera, where there are suitable habitats. The

suggestion of migration in the opposite direction involves similar objections.

If, however, trans-Wallacean migration is proposed, it seems clear that *Lasia* must have migrated from west to east, while *Cyrtosperma* must have gone from east to west. If that was the case, the Lasiinae arrived in Malesia twice, *Lasia* and *Podolasia* via India, *Cyrtosperma* on the leading

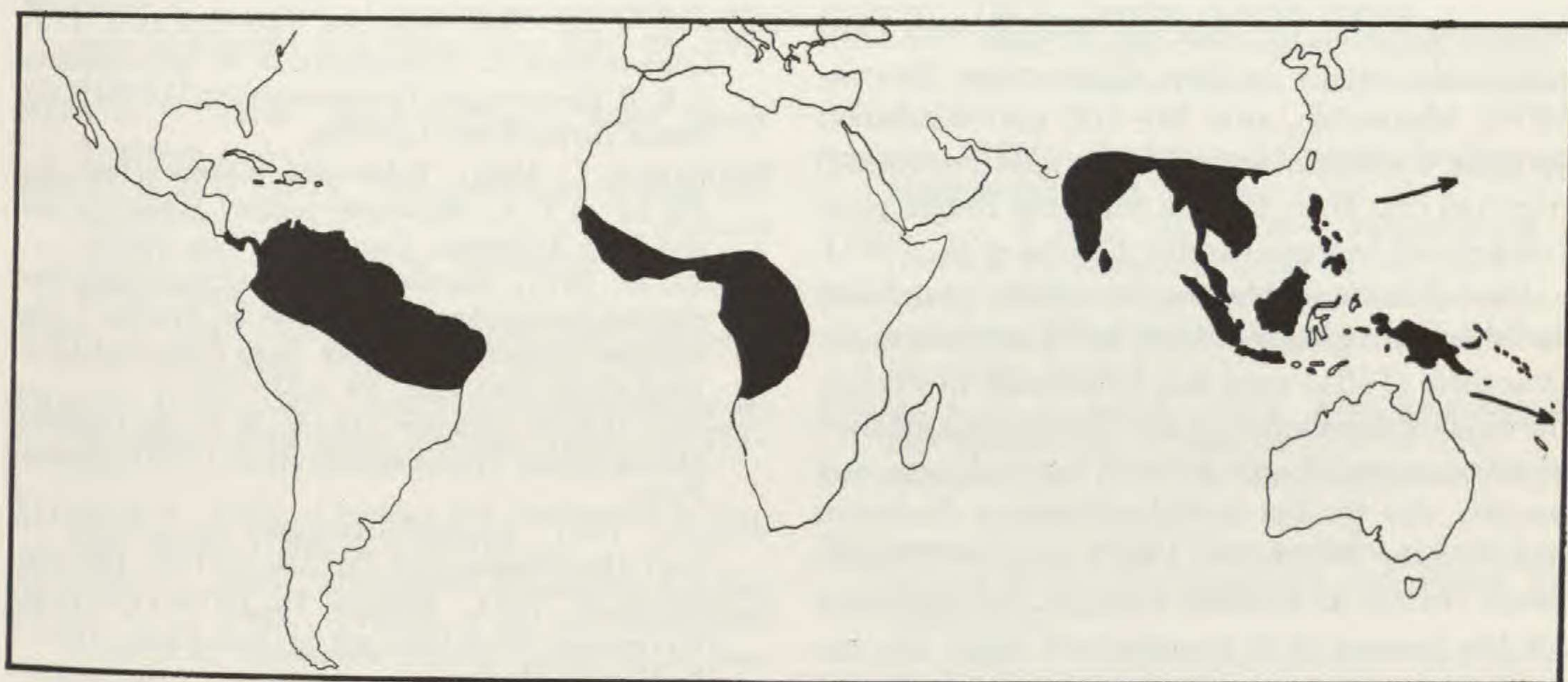


FIGURE 12. World distribution of Lasieae subtribe Lasiinae. Arrows indicate direction of extension of *Cyrtosperma* into Oceania.

edge of the Australian plate. This (and the distribution of *Lasiomorpha* and *Urospatha*) requires that proto-Lasiina predated the breakup of Gondwanaland. Bearing in mind that these genera are very closely related, it is not difficult to modify this hypothesis such that it is suggested that *Lasia* and *Cyrtosperma* had themselves already differentiated before the breakup of Gondwanaland.

Then it is argued that *Cyrtosperma* and *Lasia* have both reached Malesia twice, and that neither of them has undergone long-distance dispersal over sea. It is suggested that, already differentiated by

the time Gondwana began to fragment in the late Jurassic/lower Cretaceous, the genera of Lasiinae were distributed such that *Urospatha* rafted off on South America, and *Lasiomorpha* on Africa. In the east, the ranges of *Cyrtosperma* and *Lasia* must have straddled the Indian and Australian plates and were split as India broke away some 140–120 mya (Audley-Charles et al., 1981). Moving east and later north, the aging soils and drying climate of Australia may have provided fewer habitats for this group, which became confined to the poor archipelagic flora of the leading edge of the Aus-

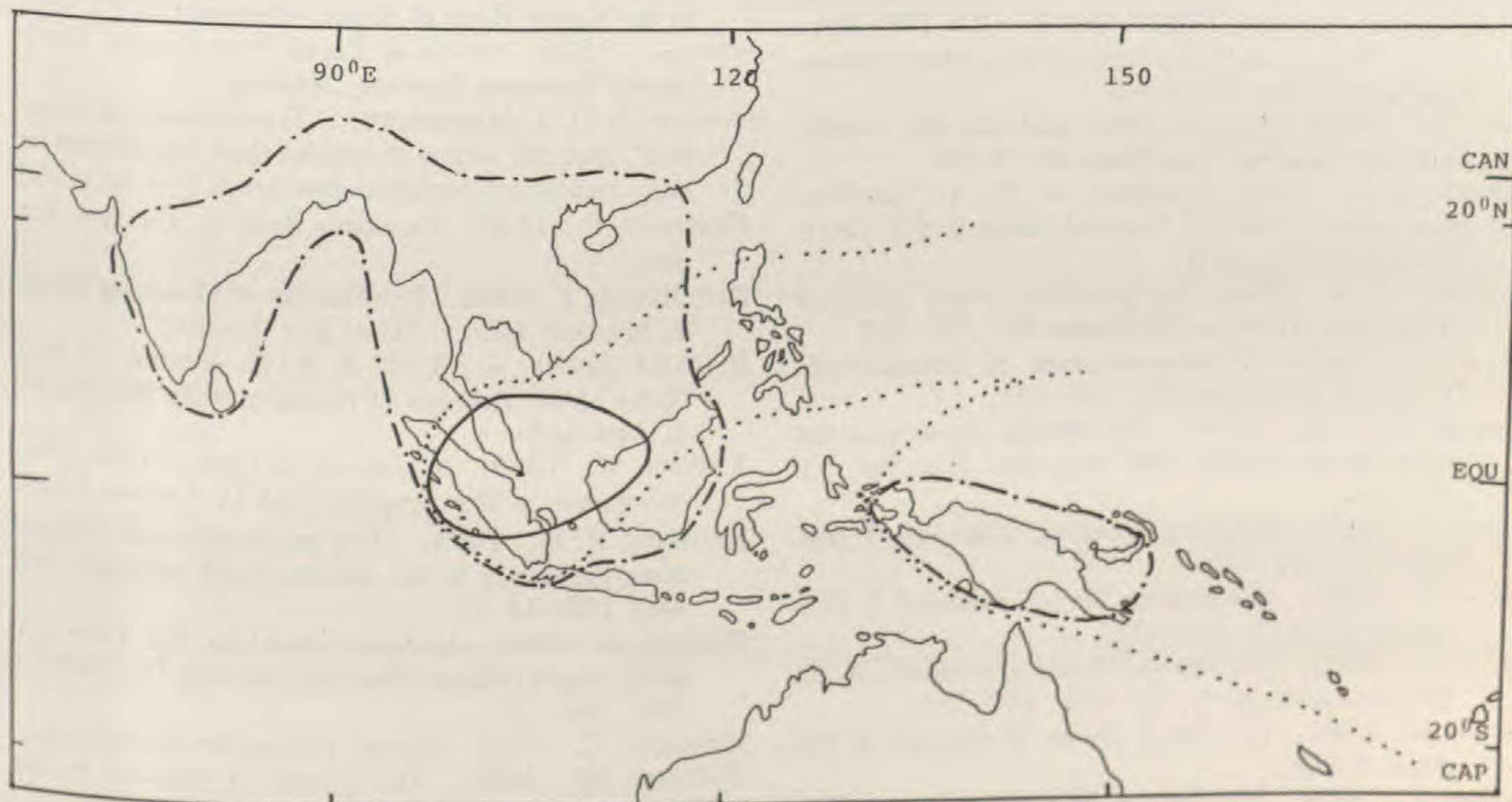


FIGURE 13. Distribution of Lasieae subtribe Lasiinae in Indomalesia. ..... = *Lasia*. — = *Podolasia*. - · - · - = *Cyrtosperma*.

tralian plate until the Miocene collision with Laurasia and orogeny in New Guinea (van Steenis, 1979). Meanwhile, after 80–100 my of isolation on India, *Cyrtosperma* and *Lasia* (and *Podolasia*) migrated into West Malesia when the Indian plate collided with Laurasia (Audley-Charles et al., 1981).

Dual arrivals in Malesia have been postulated for other plant groups of fairly low taxonomic rank: Dransfield (1981) used this hypothesis to explain the disjunct distribution of the *Clinostigma* alliance of palms, especially the genus *Rhopaloblaste*, and possibly also for the coryphoid genera *Livistona* and *Licuala*. Whitmore (1981) cited the bamboo genus *Nastus* as another example. Invoked here for the Lasieae, it is necessary to apply the hypothesis to a species—*Lasia spinosa*. As *L. spinosa* shows little tendency even to radiate over its enormous range, a period of stasis in excess of 100 my seems possible for this relict. For *Anaphyllum* and *Pycnospatha*, then, a Gondwanan origin, followed in the latter by migration and contraction in a 40-my-period seems plausible.

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